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Why cave planthoppers study matters: are Cixiidae a subtroglophile lineage? (Hemiptera, Fulgoromorpha)

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Abstract

Planthoppers are an interesting and contrasting model among insects for studying the subterranean environments. Their morphological and ethological adaptations to the underground conditions (complete darkness, lower temperatures, high hygrometry, stability of environmental constants, rarefied food sources, etc.), and their worldwide distribution in both temperate and tropical areas make them an interesting model among invertebrates. In this review, we highlight why cave planthoppers study matters, with particular emphasis on the Cixiidae. The two hypotheses proposed, the 'climatic relict hypothesis' and the 'adaptive shift', are not sufficient enough to clearly understand and explain the drivers to cavernicoly. Phylogenetic analyses approaches might help to better document and increase our knowledge on such peculiar environments. The singularity of the distribution pattern of the adaptation to cavernicoly in planthoppers raises also interesting questions to investigate and suggest contrasting scenarios to explore further, particularly should the Cixiidae be defined as a subtroglophile lineage?

Keywords

Cave, cavernicoly, hypogean, Kinnaridae, Meenoplidae, subterranean

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Introduction

When Austro-Hungarian entomologist Ferdinand Schmidt in 1832 described the first beetle species adapted to caves in Postojna Cave, Slovenia (Schmidt 1832; Polak 2005), he also revealed the existence of subterranean insect life stable and suitable. Until then unsuspected, this ability to adapt to underground life is now rich in many examples and one now recognizes a real "hidden" underground diversity where all the major phyla are now represented (Sendi et al. 2020). Indeed, since then, interest in subterranean habitats has continued to grow (Mammola 2019), with all authors emphasizing the great potential of their study and how the subterranean environment is a well-suited model for studying the processes of adaptation of organisms under various morphological, ethological or ecological perspectives (Racovitza 1907; Jeannel 1926; Vandel 1964; Poulson and Culver 1969; Howarth 1980; Gibert and Deharveng 2002). While substantial results have already been published, the subterranean world keeps fascinating and questioning scientists, who consider it a natural laboratory of well-suited models for evolutionary and ecological studies (Poulson and White 1969; Culver and Pipan 2010; Ribera et al. 2018).

Focusing on the insect fauna only, hypogean species occur in 19 of the insect orders (Romero 2009). In Hemiptera, even if the obligate phytophagous Auchenorrhyncha Fulgoromorpha would not be the first expectation in the subterranean environment (Hoch 2002), more than 60 species of planthoppers have now been described and documented as subterranean species (Bourgoin 2024). This may seem low compared to Coleoptera where the number and diversity of species are the greatest, thus concentrating the majority of the studies (Gibert and Deharveng 2002; Faille et al. 2015a; Huang 2022). However, the obligatory phytophagy constraints of planthoppers, their short-range intraspecific communication transmitted by the substrate (Claridge and Vrijer 1994), which direct their reproductive behavior, their morphological and ethological adaptations to the underground conditions (complete darkness, lower temperatures, high hygrometry, stability of environmental constants, rarefied food sources, etc.), and their worldwide distribution in both temperate and tropical areas, make planthoppers an interesting and contrasting model among insects for studying the subterranean environments.

Based on these singularities, the purpose of this review is to summarize our current knowledge on cave planthoppers, with particular emphasis on the Cixiidae. We point to possible future research perspectives by using these taxa as models to further explore the mechanisms of adaptation to a highly restrictive environment, and by documenting the resulting phylogenetic patterns we observe (Barr 1968; Protas and Jeffery 2012; Howarth and Moldovan 2018a; Soares and Niemiller 2020; Huang 2022).

Materials and methods

When examining subterranean ecosystems, and in contrast to the surface-dwelling species inhabiting epigean habitats, two primary categories of inhabitants are distinguished: soil-dwelling species residing in endogeic habitats, and cave-dwelling species residing in hypogean habitats. Among the cave-dwelling species, numerous authors have attempted to

categorize them based on various criteria such as morphological, physiological, ethological, or ecological (summarized in Howarth and Moldovan 2018b). However, adaptability to underground environments exists along a continuum. Consequently, regardless of the chosen classification criterion, whether it be, subjectivity often prevails. In this review, we will follow Sket's 2008 classification, rooted in the "Schiner-Racovitza classification" (Trogloxene / Troglophile / Troglobiont), which is considered the foundation for all subsequent categorizations (Horvath and Moldovan 2018b), with the following definitions:

- Troglobiont species strongly linked to underground ecosystems.
- Eutroglophile species, epigean but able to maintain a permanent subterranean population.
- Subtroglophile species perpetually or temporarily inhabiting a subterranean habitat but linked to the epigean habitats for some biological functions.
- Trogloxene species occurring sporadically in a hypogean habitat and unable to maintain a subterranean population.

The map was built using the software QGIS 3.10.2 and we used the climate zones proposed by van Velthuisen et al. in 2007.

What do we know about cave planthoppers?

Geographic distribution

The first cave-dwelling planthopper was mentioned in 1907 by the Rumanian biologist Emil Racovitza who reported the observation of an unpigmented cixiid planthopper which he identified as "*Cixius* sp." from the Balearic Island of Mallorca (Racovitza 1907). Unfortunately, the species was not described formally, and there is no record of any voucher specimens. Only nearly half a century later, another subterranean planthopper species was found in Zimbabwe. The species displays distinct modifications from epigean species, such as the lack of ocelli and obsolete compound eyes, vestigial, pad-like tegmina and light body pigmentation. It was reported as "a subterranean maggot-like planthopper" (China and Fennah 1952: 189), living in the soil, apparently feeding on roots of maize and tobacco, and being tended by ants. The species was so much modified, that it could not be accommodated in any of the existing Fulgoromorpha families, it was described in a new family, Hypochthonellidae China & Fennah, 1952, for *Hypochthonella caeca* China & Fennah, 1952. The genus to date remains monospecific.

Since then, cavernicolous planthopper species have been discovered from many parts of the world (Fig. 1): Argentina, Australia and New Zealand, Brazil, Canary Islands, Hawaii, Mexico, Madagascar and La Réunion and several countries in Europe (Croatia, France, Italy, Slovenia, Spain, France) (Fig. 1). To date, 70 planthopper species in five planthoppers families have been explicitly reported to live in the subterranean ecosystems (Table 1): Cixiidae Spinola, 1839 (44 species), Delphacidae Leach, 1815 (3 species), Meenoplidae Fieber, 1872 (14 species), Kinnaridae Muir, 1925 (7 species), Hypochthonellidae (1 species) and

Table 1. The cave-dwelling species.

Family	Species	Authorship	Subterranean habitat	Type locality	Ecological category
Cixiidae	*Borysthenes hainanensis*	Lyu & Webb, 2023	Lava tube and epygean	Quishierdong lava tube, Haikou, Hainan, China	Eutroglophile
Cixiidae	*Brixia briali*	Hoch & Bonfils, 2003	Lava tube	Caverne de la tortue, La Réunion	Troglobiont
Cixiidae	*Celebenna thomarosa*	Hoch & Wessel, 2011	Limestone cave	Gua Assuloang, Maros karst, Sulawesi, Indonesia	Troglobiont
Cixiidae	*Cixius actunus*	Hoch, 1988	Limestone cave	Cueva de las Maravillas, Oaxaca, Mexico	Troglobiont
Cixiidae	*Cixius ariadne*	Hoch & Ashe, 1993	Lava tube	Cueva de la Curva, El Hierro, Canary Islands	Troglobiont
Cixiidae	*Cixius azopicavus*	Hoch, 1991	Lava tube	Furna de Agostinha, Pico, Azores	Troglobiont
Cixiidae	*Cixius cavazoricus*	Hoch, 1991	Lava tube	Furna dos Concheiros, Faial, Azores	Troglobiont
Cixiidae	*Cixius nycticolus*	Hoch & Ashe, 1993	Lava tube	Cueva Roja, El Hierro, Canary Islands	Troglobiont
Cixiidae	*Cixius orcus*	Fennah, 1973	Limestone cave	Cueva de Emilia, Queretaro, Mexico	Troglobiont
Cixiidae	*Cixius palmeros*	Hoch & Ashe, 1993	Lava tube	Cueva de los Palmeros, La Palma, Canary Islands	Troglobiont
Cixiidae	*Cixius pinarcoladus*	Hoch & Ashe, 1993	Lava tube	Cueva del Diablo, La Palma, Canary Islands	Troglobiont
Cixiidae	*Cixius ratonicus*	Hoch & Ashe, 1993	Lava tube	Cueva del Raton, La Palma, Canary Islands	Troglobiont
Cixiidae	*Cixius tacandus*	Hoch & Ashe, 1993	Lava tube	Cueva de Tacande, La Palma, Canary Islands	Troglobiont
Cixiidae	*Coframalaxius bletteryi*	Le Cesne & Bourgoin, 2022	Limestone cave	Grotte de la Chèvre d'Or, Alpes-Maritimes, France	Troglobiont
Cixiidae	*Confuga persephone*	Fennah, 1975	Limestone cave	Council cave, Takaka, Nelson province, New Zealand	Troglobiont
Cixiidae	*Ferricixius davidi*	Hoch & Ferreira, 2012	Ferrugenous cave	MP-08 cave, Itabirito, Minas Gerais state, Brazil	Troglobiont
Cixiidae	*Ferricixius goliathi*	Santos, Hoch & Ferreira, 2023	Ferrugenous cave	ABOB-0043 cave, Nova Lima, Minas Gerais state, Brazil	Troglobiont
Cixiidae	*Ferricixius michaeli*	Santos, Hoch & Ferreira, 2023	Limestone cave	ICMAT-0053 cave, Matozinhos, Minas Gerais state, Brazil	Troglobiont
Cixiidae	*Ferricixius urieli*	Santos, Hoch & Ferreira, 2023	Quartz	Casas cave, Lima Duarte, Minas Gerais state, Brazil	Subtroglophile
Cixiidae	*Ibleocixius dunae*	D'urso & Grasso, 2009	Limestone cave	Iblei mountains, Sicily	Troglobiont
Cixiidae	*Iolania frankanstonei*	Hoch & Porter, 2024	Lava tube	Kipuka Kanohina system, Hawaii	Troglobiont
Cixiidae	*Notolathrus sensitiva*	Remes-Linecov, 1992	Limestone cave	Caverna del Arenal, sistema de Cuchillo Cura, Neuquen, Argentina	Troglobiont
Cixiidae	*Oliarus gagnei*	Hoch & Howarth, 1999	Lava tube	Ulupalakua cave, Maui Island, Hawaii	Troglobiont
Cixiidae	*Oliarus hernandezi*	Hoch & Izquierdo, 1996	Lava tube	Finch cave, Floreana Island, Galapagos	Troglobiont
Cixiidae	*Oliarus kalaupapae*	Hoch & Howarth, 1999	Lava tube	Fisherman Shak's cave #1, Molokai Island, Hawaii	Troglobiont
Cixiidae	*Oliarus lorettae*	Hoch & Howarth, 1999	Lava tube	Ana Lima Kipo lava tube, Kiholo bay, Hawaii	Troglobiont
Cixiidae	*Oliarus makaiki*	Hoch & Howarth, 1999	Lava tube	Yellow Jacket cave, Hualalai volcano, Hawaii	Troglobiont
Cixiidae	*Oliarus polyphemus*	Fennah, 1973	Lava tube	Bird Park cave, Kipuka Puaulu, Hawaii	Troglobiont
Cixiidae	*Oliarus priola*	Fennah, 1973	Lava tube	Holoinawawai stream cave, Maui Island, Hawaii	Troglobiont
Cixiidae	*Oliarus waikau*	Hoch & Howarth, 1999	Lava tube	Waikau cave, Maui Island, Hawaii	Troglobiont
Cixiidae	*Sanghabenna florenciana*	Hoch & Bourgoin, 2017	chaos of granite blocks	Hon Ba massif, Vietnam	Subtroglophile
Cixiidae	*Solonaima baylissa*	Hoch & Howarth, 1989	Lava tube	Bayliss cave, Mt Surprise, Queensland, Australia	Troglobiont

Family	Species	Authorship	Subterranean habitat	Type locality	Ecological category
Cixiidae	*Solonaima halos*	Hoch & Howarth, 1989	Limestone cave	Queenslander cave, Chillagoe, Queensland, Australia	Troglobiont
Cixiidae	*Solonaima irvini*	Hoch & Howarth, 1989	Limestone cave	Swiftlet scallops cave, Chillagoe, Queensland, Australia	Troglobiont
Cixiidae	*Solonaima pholetor*	Hoch & Howarth, 1989	Limestone cave	Royal Arch cave, Chillagoe, Queensland, Australia	Troglobiont
Cixiidae	*Solonaima stonei*	Hoch & Howarth, 1989	Limestone cave	Arena cave, Chillagoe, Queensland, Australia	Troglobiont
Cixiidae	*Solonaima sullivani*	Hoch & Howarth, 1989	Limestone cave	Crystal cascades cave, Mt Mulgrave station, Queensland, Australia	Troglobiont
Cixiidae	*Tachycixius crypticus*	Hoch & Ashe, 1993	?	Palo blanco, Tenerife, Canary Islands	Troglobiont
Cixiidae	*Tachycixius lavatubus*	Remane & Hoch, 1988	Lava tube	Cueva Grande de Chio, Tenerife, Canary Islands	Troglobiont
Cixiidae	*Tachycixius retrusus*	Hoch & Ashe, 1993	?	Barranco de Ijuana, Tenerife, Canary Islands	Troglobiont
Cixiidae	*Trigonocranus emmeae*	Fieber, 1876	Endogean and epygean	Emme valley, Switzerland	Eutroglophile
Cixiidae	*Trirhacus helenae*	Hoch, 2013	Dolomite cave	Spilja kod Nerezinog dola, Mljet Island, Croatia	Troglobiont
Cixiidae	*Typhlobrixia namorokensis*	Synave, 1953	Limestone cave	Namoroka karst, Madagascar	Troglobiont
Cixiidae	*Undarana collina*	Hoch & Howarth, 1989	Lava tube	Collins 210 cave, Mt Surprise, Queensland, Australia	Troglobiont
Cixiidae	*Undarana rosella*	Hoch & Howarth, 1989	Lava tube	Bayliss cave, Mt Surprise, Queensland, Australia	Troglobiont
Delphacidae	*Notuchus kaori*	Hoh & Ashe, 2006	Endogean	Pic du grand Kaori, New Caledonia	Troglobiont
Delphacidae	*Notuchus larvalis*	Fennah, 1980	Limestone cave	Taphozous cave, Hienghène, New Caledonia	Troglobiont
Delphacidae	*Notuchus ninguae*	Hoch & Ashe, 2006	Endogean	Pic Ningua, New Caledonia	Troglobiont
Flatidae	*Budginmaya eulae*	Fletcher, 2009	Endogean	Nid de *Camponotus*, Bandalup Hill, Western Australia	Troglobiont
Hypochthonelidae	*Hypochthonella caeca*	China & Fennah, 1952	Endogean	Salisbury, Southern Zimbabwe	Troglobiont
Kinnaridae	*Iuiuia caeca*	Hoch & Ferreira, 2016	Limestone cave	Lapa de Baixão cave, Bahia, Brazil	Troglobiont
Kinnaridae	*Oeclidius antricola*	Fennah, 1980	Limestone cave	Jackson Bay cave, Clarendon, Jamaica	Troglobiont
Kinnaridae	*Oeclidius hades*	Fennah, 1973	Limestone cave ?	Cueva de Valdosa, San Luis Potosi, Mexico	Troglobiont
Kinnaridae	*Oeclidius minos*	Fennah, 1980	Limestone cave	Jackson Bay cave, Clarendon, Jamaica	Troglobiont
Kinnaridae	*Oeclidius persephone*	Fennah, 1980	Limestone cave	Portland caves, Clarendon, Jamaica	?
Kinnaridae	*Kinnapotiguara troglobia*	(Hoch & Ferreira, 2013)	Limestone cave	Gruta do troglobio, Rio Grande do Norte, Brazil	Troglobiont
Kinnaridae	*Valenciolenda fadaforesta*	Hoch & Senda, 2021	Dolomitic cave	Valencia, Vilamarxant, 'Murceliagos' cave, Spain	Troglobiont
Meenoplidae	*Eponisia hypogaea*	Hoch, 1996	Limestone cave	Grottes d'Adio, New Caledonia	Troglobiont
Meenoplidae	*Meenoplus cancavus*	Remane & Hoch, 1988	Lava tube	Cueva Don Justo, El Hierro, Canary Islands	Troglobiont
Meenoplidae	*Meenoplus charon*	Hoch & Ashe, 1993	Lava tube	Cueva de la Curva, El Hierro, Canary Islands	Troglobiont
Meenoplidae	*Meenoplus claustrophilus*	Hoch & Ashe, 1993	Lava tube	Cueva del Raton, La Palma, Canary Islands	Troglobiont
Meenoplidae	*Meenoplus roddenberryi*	Hoch & Naranjo, 2012	Lava tube	Minas los Roques, Gran Canaria, Canary Islands	Troglobiont
Meenoplidae	*Nisia subfogo*	Hoch & Oromi, 1999	Lava tube	Caldera de Fogo, Fogo, Cape Verde Islands	Troglobiont

Family	Species	Authorship	Subterranean habitat	Type locality	Ecological category
Meenoplidae	*Phaconeura capricornia*	Hoch, 1990	Limestone cave	Swiss cheese cave, Cape York, Queensland, Australia	Troglobiont
Meenoplidae	*Phaconeura crevicola*	Hoch, 1990	Limestone cave	Raindance cave, Queensland, Chillagoe, Australia	Troglobiont
Meenoplidae	*Phaconeura minyamea*	Hoch, 1990	Limestone cave	Tea tree cave, Queensland, Chillagoe, Australia	Troglobiont
Meenoplidae	*Phaconeura mopamea*	Hoch, 1990	Limestone cave	Carpentaria cave, Queensland, Chillagoe, Australia	Troglobiont
Meenoplidae	*Phaconeura pluto*	Fennah, 1973	Limestone cave	Quandong cave, Nambung national park, Western Australia	Troglobiont
Meenoplidae	*Phaconeura proserpina*	Hoch, 1993	Limestone cave	Cave C-215, North west cape peninsula, Western Australia	Troglobiont
Meenoplidae	*Suva oloimoa*	Hoch & Ashe, 1988	Lava tube	Oloimoa cave, Savai'i Island, Samoa	Troglobiont
Meenoplidae	*Tsingya clarkei*	Hoch & Wessel, 2014	Limestone cave	Anjohy Manitsy, Tsingy de Bemaraha, Madagascar	Troglobiont

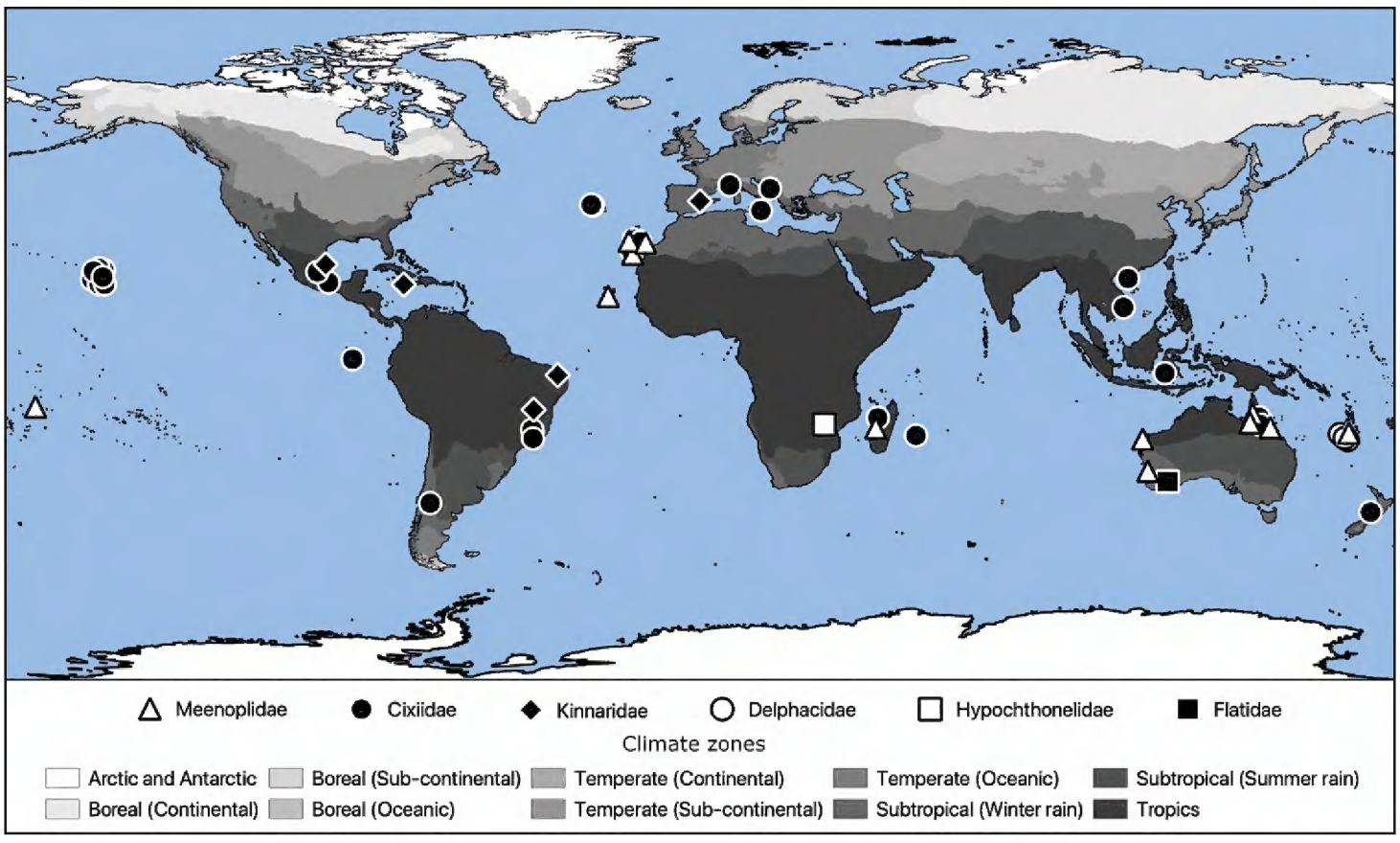

Figure 1. Distribution map of the cave-dwelling planthoppers according to main world ecoregions.

Flatidae (1 species) (Hoch 1994; Hoch 2013, and references therein; Bourgoin 2024). A species of Flatidae from Australia, discovered under conditions similar to those of *H. caeca* – within an ant nest beneath a rock, exhibiting "morphological adaptations akin to those observed in cave-dwelling planthoppers" (Fletcher and Moir 2009) – is also included in this list. Most of these species (58 species) are true troglobionts exhibiting troglomorphies being adaptations correlated with cavernicoly.

Obviously, it is very likely that many new species remain to be discovered as numerous vast known cave systems all around the world are still to be explored (Hoch 2002). Only in the past two decades many new discoveries were reported from Papua New Guinea (Hoch 2002), Brazil (Hoch and Ferreira 2012, 2016; Souza Silva et al. 2020; Santos et al. 2023), Madagascar (Hoch et al. 2014), Vietnam (Hoch et al. 2017),

and even in better explored areas in Europe such as in Italy (D'Urso and Grasso 2009), Canary Islands (Hoch et al. 2012), Croatia (Hoch 2013), Spain (Hoch et al. 2021), or France (Le Cesne et al. 2022).

Phylogenetic patterns of cavernicoly in planthoppers

With few exceptions, only two main lineages within the Fulgoromorpha, the Cixiidae and the Meenoplidae-Kinnaridae have succeeded in colonizing underground ecosystems. These belong to two different superfamilies (Delphacoidea and Fulgoroidea respectively) (Bourgoin and Szwedo 2023) and are therefore phylogenetically independent (Bucher et al. 2023). Both are regarded as groups of epigean species, with larval instars feeding on roots known to be living close to or inside the soil (Hoch 1994, 2002; Wessel et al. 2007; Bowser 2014; Bartlett et al. 2018). Particularly in Cixiidae, all basal lineages and several tribes (Luo et al. 2021; Bourgoin et al. 2023a) are represented: Bennini Metcalf, 1938 (2 species), Brixiini Emeljanov, 2002 (9 species), Cixiini Spinola, 1839 (16 species), Oecleini Muir, 1922 (4 species), Pentastirini Emeljanov, 1971 (8 species), Pintaliini Metcalf, 1938 (1 species).

Aside from these three families, three cavernicolous Delphacid species, all belonging to the same genus *Notuchus* Fennah, 1969 from New Caledonia should also be mentioned. Interestingly and as for several cixiid species also (Bourgoin et al. 2023b), at least two of them are being tended by ants (see Hoch et al. 2006) such as the Hypochthonellid species. The latter displays so many troglomorphic characters (depigmented, micropterism, blindness, maggot-like habitus) that until now, the family remains unplaced and might be related to Flatidae (Bartlett et al. 2018). Another Western Australian flatid species, *Budginmaya eulae* Fletcher & Moir, 2009, also tended by ants, exhibits reduction of the tegmina, hindwings and eyes, pale coloration and increased number of setae on the head, body, tegmina and legs (Fletcher and Moir 2009).

Cavernicolous planthopper biology

Environment

The subterranean biome ranges from the 'Milieu Souterrain Superficiel' (MSS, Juberthie et al. 1980), a 'network of empty air-filled voids and tiny cracks developed between rock fragments' under the topsoil (also often referred as the Mesovoid Shallow Substratum, Mammola et al. 2016), to narrow dark rifts and crevices, more or less deep wells, connected or not to the surface (extended transition zone), to small entirely lightless, interconnected voids and cavities of the 'Milieu Souterrain Profond' (MSP, Juberthie 1983) to caves. These can reach large dimensions and extensions, up to several meters high and many kilometers of passage (e.g., Allred and Allred 1997). Subterranean planthoppers have been found in this wide variety of subterranean ecosystems, provided that roots are extant and relative humidity is high (Hoch 1994, 2002). These roots, usually developed in the topsoil and the MSS, can develop deeper, emerging in the caves from cracks forming long strands hanging from the ceiling of the cave, or form a fine root network running

over the walls and floor of the cave (Fig. 2) such as in limestone caves, lava tubes, and also in granitic chaos (Table 1). As strictly phytophagous insects, the cave-dwelling planthoppers are primary consumers in the subterranean ecosystems (Hoch and Howarth 1993).

Knowledge of cave-dwelling planthoppers remains generally limited to the description of the species. Much of what we know about the biology of cavernicolous planthoppers comes from a single case study on the blind, flight- and pigmentless *Oliarus polyphemus* Fennah from Hawaii Island (Hoch and Howarth 1993). Field observations on various aspects of the biology of other species are still scarce (e.g., Hoch and Asche 1993; Hoch et al. 2006, 2014, 2021; Soulier-Perkins et al. 2015; Le Cesne et al. 2022, 2023).

The roots system of the plants provides them with a relatively abundant food but limited by an epigean flora developing long roots, which however confine them to the environment of shallow caves. These roots are also an ideal medium to communicate with the other individuals, in particular to meet mating partners as in an epigean life. Indeed, as with their epigean relatives (Claridge 1985), cave planthoppers produce low-frequency, substrate-borne vibrations to communicate. This behavior, which is general in planthoppers (Soulier-Perkins et al. 2015) and relies on this communication channel for their mating behavior (Hoch 2002), has been confirmed and analyzed (*in-* and *ex-situ*) on several occasions with these cavernicolous species (Hoch and Howarth 1989b; Hoch and Howarth 1999; Hoch and Wessel 2006; Soulier-Perkins et al. 2015). As with epigean species (Hoch 2002; Soulier-Perkins et al. 2015), it has been suggested that this behavior would allow them to locate a potential mate also in the permanent darkness of caves. However, as with epigean species, one cannot exclude other behaviors such as possible territorial rivalry between males (Soulier-Perkins et al. 2015).

While the eyes of adult cave-dwelling species are often reduced or absent, the antenna remains well developed, especially with the characteristic large olfactory placoid sensilla on the pedicel in planthoppers (Hoch et al. 2006; Santos et al. 2023). As already shown in several epigean species (Aljunid and Anderson 1983; Young 2002; Riolo et al. 2012), their role in the search for food roots via plant volatile compounds is likely, while their role for other intraspecific interactions, possibly pheromone-driven, cannot be ruled out (Wang et al. 2018), although experimental evidence is lacking.

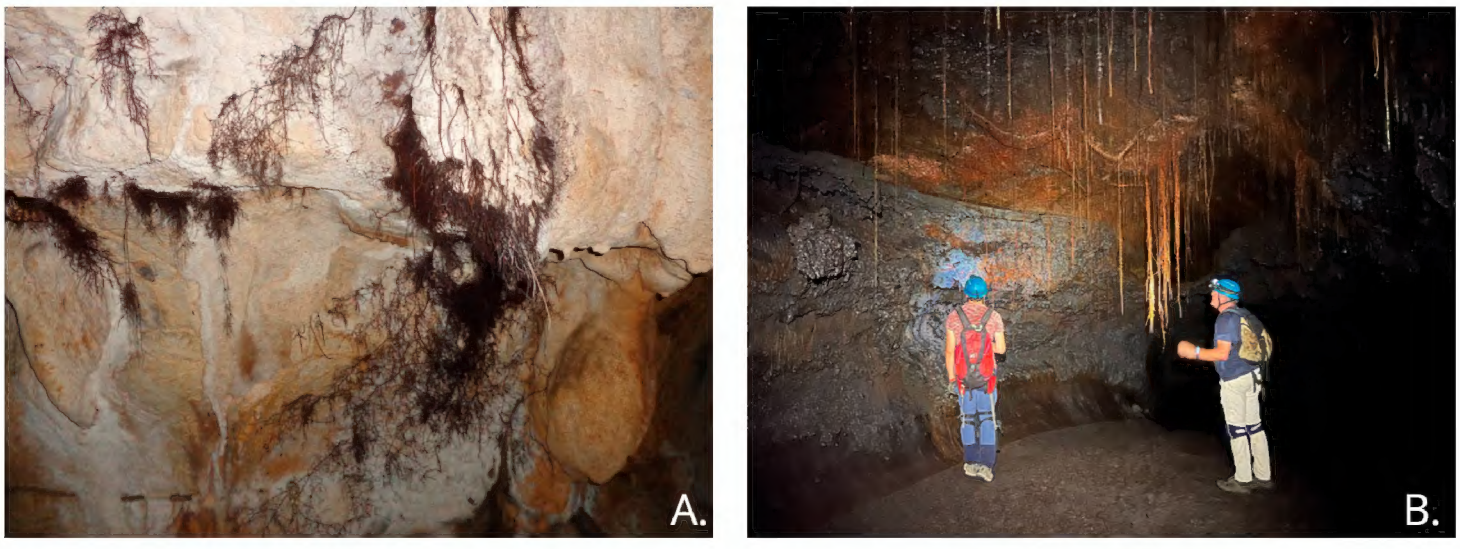

Figure 2. A roots along the wall in a limestone cave of the south of France (Grégoire Maniel) **B** roots hanging from the ceiling of a lava tube in La Réunion (Fred Melon).

Reproduction, life history and postembryonic development

It has been observed that females of the troglobitic *Oliarus polyphemus* from Hawaii lay very few eggs, suggesting a low reproduction rate, a typical K-selection process found in ecologically stable environments (Hoch and Howarth 1993) and documented for many obligate cave species (Culver 1982). *Oliarus'* eggs are deposited in a wax-filament nest on roots. The nymphs are usually found close to the roots while the adults are generally active and found throughout the cave (Hoch and Howarth 1993). In contrast, adults of *Coframalaxius* Bourgoin & Le Cesne, 2022, from Southern France were found together inside the waxy nests, little active, while nymphs were found active throughout the cave, close to other roots (Le Cesne et al. 2022). In *Typhlobrixia* Synave, 1953, both nymphs and adults were observed in isolation within the Tsingy Namoroka cave system in Madagascar, indicating that both are potential dispersal stages. However, adults were also frequently encountered in close proximity to roots (Soulier-Perkins et al. 2015).

Although the nymphal morphology even of epigean Cixiidae is not well-documented, it is reported that their first instars have very low pigmentation and are either blind or possess only a few ommatidia. The development of their compound eyes begins only after the third or fourth instar (Wilson and Tsai 1982; Wilson et al. 1983; personal observation of the authors). Although a comprehensive description of all nymphal instars of the troglobiont kinnarid *V. fadaforesta* Hoch & Sendra, 2021 has been recently published (Ortega-Gomez et al. 2022), which reports the absence of eyes and ocelli since the first instar, the nymphal morphology of epigean Meenoplidae-Kinnaridae nymphs remains unknown, a fact which impairs a direct comparison.

Colonisation and evolution

Two hypotheses have been proposed to explain the evolution of cavernicoly. The "climatic relict hypothesis" (CRH) was initially proposed by Vandel in 1964 (Barr 1968), and further developed by Peck and Finston (1993). It suggests that the presence of troglobionts can be attributed to past changes in epigean abiotic factors, such as climatic changes, which constrained epigean species and driven them to colonize subterranean habitats as refuges. According to this hypothesis, it is expected that the insects that colonized subterranean habitats do not have any extant close relatives today (Fig. 3, CRH), as those close relatives were unable to adapt to the changes in epigean abiotic factors or are at least allopatrically distributed compared to the cave-dwelling species (Wessel et al. 2007).

On the other hand, Howarth (1980, 1983) proposed the "adaptive shift hypothesis" (ASH), which suggests that cavernicolous animals are present in suitable subterranean areas due to active colonization of subterranean habitats as new niches through "adaptive shifts" of epigean species. According to this hypothesis, one would expect to observe hypogeal species that are closely related to their epigean counterparts in a parapatric distribution (Wessel et al. 2007) (Fig. 3, ASH).

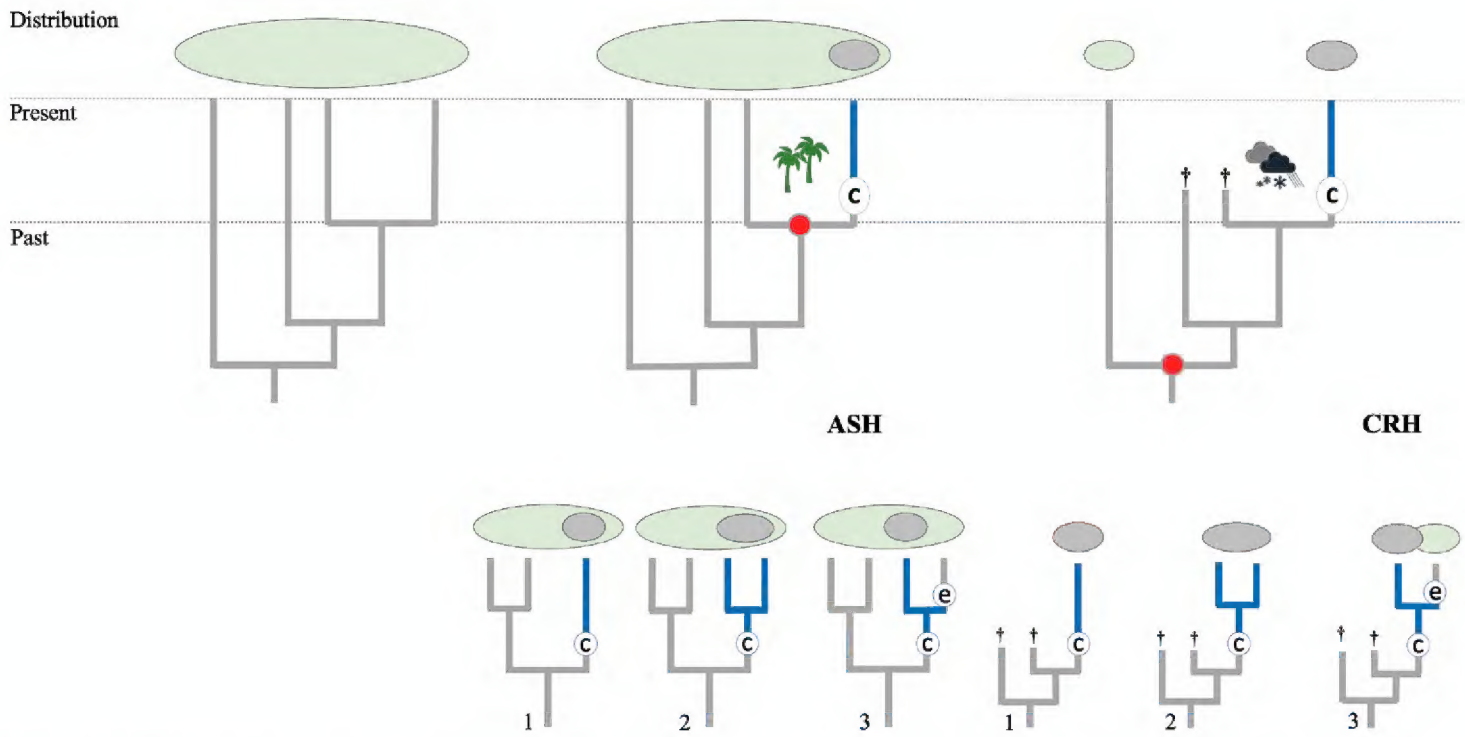

Figure 3. Resulting distributions and phylogenies of closely related species with one species moved to cavernicoly (C), according the two explanatory models, the 'Adaptive Shift Hypothesis' (ASH) or the 'Climatic Relict Hypothesis' (CRH). with possible subsequent scenarios: in-cave speciation (ASH 2, CRH 2) or possible return to epigean (E) conditions (ASH 3, CRH 3). Red circle denotes the node of the first common ancestor linking the cave species and its closest extant epigean relative.

To determine which of the two explanatory models applies in a given case, Wessel & al (2007) suggested that a phylogenetic analysis of the faunas should be undertaken: an allopatric or parapatric speciation will respectively accredit the "climatic relict" or "adaptive shift" model as a possible speciation process explanatory hypothesis (Fig. 3).

Why do cave planthopper studies matter?

Planthoppers in light of definitions: the limits of morphological and etho-ecological classifications

The first classification of cave organisms was based on their degree of morphological adaptation to the hypogean habitats (Shiner 1854) and adapted by Racovitza in 1907 who recognized three categories: the trogloxenes (temporary visitors to caves), the troglophiles (facultatively cavernicolous) and the troglobionts (obligately cave-dwelling species). However, the transitional category troglophile has always been difficult to define. Reviewing the century of evolution of the subterranean organism's classification, Sket (2008) proposed an ecology-based terminology. Accordingly, subterranean species are now standardly classified as true cavernicolous or troglobionts (species strictly bound to the hypogean habitats), eutroglophiles (epigean species able to maintain permanent hypogean populations), subtroglophiles (epigean species living temporally or cyclically during their life in hypogean conditions) and trogloxenes (species occurring sporadically in a hypogean habitats, unable to establish subterranean stable populations) (Sket 2008; Howarth and Moldovan 2018b).

Just as the degree of troglomorphy appeared to be a criterion difficult to apply for classifying subterranean organisms, Wessel et al. (2007) and Hoch et al. (2014) have shown that it is neither a reliable indicator for the age of the cavernicolous lineage, which in Hawaii and Australia for instance, does not necessarily correlate with the age of cave. Moreover, if cave-adaptation and troglomorphies are strongly linked to the troglobiont category of Sket (2008), the opposite is not true and a troglobiont species does not necessarily exhibit troglomorphies. Indeed, it might be not that common, but some species found in caves without troglomorphies although never found at the surface, might have been called trogloxene when they might be true troglobiont or at least eutroglophile as pointed out by Deharveng et al. (2022).

From Sket's 2008 etho-ecological perspective, and for obligatory phytophagous insects such as planthoppers, the root system of the epigean vegetation offers the opportunity to access the underground environment in temporary, cyclical or even permanent hypogean conditions. In Cixiidae for instance, the nymphs of most if not all epigean species live underground: should we consider them as subtroglophile species living cyclically during their life in hypogean conditions? e.g. does Cixiidae (as well as Meenoplidae-Kinaridae) be considered as a subtroglophile taxa, a subtroglophile family rank lineage?

Although the Sket's 2008 new classification represents a progress in better classifying undergrounds organisms offering a more precise and less arbitrary grouping system, it still leaves place to some ambiguities (Howarth and Moldovan 2018b). Neither do Sket's 2008 ecological categories constitute an evolutionary gradient pointing towards a fully adapted cave-dwelling species.

Moreover, with time during its evolutionary history, each species continues their evolution according to the ecological opportunities of its immediate environment and to adapt towards new epigean, hypogean or mixed environments. Cave adaptation is not a dead-end road of evolution. A well-studied example of such subterranean speciation exists in the Hawaiian cave planthopper *Oliarus polyphemus*. It has been demonstrated that morphologically similar, yet behaviorally distinct populations of this blind, unpigmented and flightless taxon from lava tubes on the Big Island of Hawaii, in fact are a complex of at least 12 closely related, but reproductively isolated species (Hoch and Howarth 1993; Wessel et al. 2013). Most likely they are the result of a non-adaptive radiation triggered by the rapid vegetational succession on active volcanoes.

In contrast, a true troglobiont population might also be able to evolve again into a surface-dwelling species if conditions permit, as has been described for crickets (Desutter-Grandcolas 1993: fig. 2).

In summary, it can be stated that, the degree of troglomorphy is not indicative of a phylogenetically older lineage, nor does it necessarily express a *per se* adaptation to hypogean life, nor is troglobiosis an evolutionary dead end of an evolutionary lineage.

Instead, the degree of troglomorphy has been shown to correlate with the special conditions of the environment (Hoch and Howarth 1989a, b). In the Australian cixiid genus *Solonaima*, four separate independent cave invasions have been documented from lime stone caves and lava tubes in Queensland (Hoch and Howarth 1989b). The cavernicolous *Solonaima* species display varying degrees troglomorphy, ranging from mild eye-, pigmen-

tation-, and wing reduction to the partial or entire loss of compound eyes, pigmentation and wings. Ages of caves range from 190 000 year-old lava tubes (Undara) to 5 million year-old limestone caves (Chillagoe Karst). Interestingly, the least modified (facultative) cave species occur in the geologically oldest, most eroded and comparatively open caves, those with intermediate degrees of troglomorphy in deeper caves, and while the most highly modified species, *Solonaima baylissa* Hoch & Howarth, 1989, is restricted to damp passages with high CO_2 levels in the deep cave zone of the younger lava tubes in Undara.

Whether based on morphology or etho-ecology, these classification systems remain imperfect (Howarth and Moldovan 2018b). In addition, they only take into account morphologies or life traits that have already been achieved for adaptation to troglodytic life, a way of life that could have started well before. How can we better take into account this "elusive" period from a morphological and ecological point of view? The physiological adaptations of organisms to obligately cavernicolous life probably precede the completed morphological and ecological transformations that we observe. These adaptations are also diverse, probably not all concomitant, nor necessarily biologically linked at the start: adaptations to small variations in temperature, to 'warm' tropical caves or 'cold' ones in temperate environments, to the absence of circadian rhythm, to the absence of light, to high humidity, to scarcity of resources, etc. Trying to integrate them into the classification system of cave organisms and that of their type of environment (Howarth and Moldovan 2018a, b), remains a major challenge to better understand and more precisely analyze the drivers of cavernicoly.

Planthoppers, cavernicoly and evolutionary processes: the limits of the two hypotheses

In theory the two scenarios proposed by Vandel (1964) and Howarth (1980) could logically explain the observed distributions of cave species and their closest related taxa. For instance, the active speciation highlighted by Wessel et al. (2013) of the cavernicolous *Oliarus* species of the young Hawaiian lava tube system rather fits the criteria of an adaptive shift (Howarth 1980, 1983). On the contrary, the recently described kinnarid *Valenciolenda* species Hoch & Sendra, 2021 from Spain (Hoch et al. 2021), being the only species of this family from the western continental Palearctic, would suggest a pattern of distribution that would fit with a speciation process following the relict hypothesis of Vandel (1964).

However, this may have been more complicated in reality, where several events may have taken place between the time of the first evolution of a species to cavernicoly and the current observation of the distributions of the closely related lineages. What can happen once an organism has adapted to underground habitats? 1) it can continue to diversify in the underground environment and new speciations take place (Hoch and Howarth 1993; Wessel et al. 2013; Huang 2022) (Fig. 3 ASH2 and CRH2), or 2) it can continue to diversify and might recolonize above ground habitats (Desutter-Grandcolas 1993) (Fig. 3 ASH3 and CRH3). With such possible scenarios Fig. 3 shows that the observed distributions would not be sufficient alone to discriminate between the different possible scenarios.

It should be noted that the climatic relict hypothesis and the adaptive shift hypothesis are not mutually exclusive. From a theoretical point of view, however, a clear distinction must be made between pattern (distribution) and process (factors driving speciation). The distribution patterns we see today must not necessarily reflect the processes which favored adaptations to novel environments such as subterranean habitats, e.g., MSS or caves. It is conceivable that in a given biotope cave adaptation through an adaptive shift could be followed by totally independent severe climatic constraints that would eliminate the related epigean species. Such a scenario could also bias distribution observations and would mistakenly favor the relict model as the selected process to explain the pattern observed. Even if past cave colonization events could be correlated by calibrated phylogenies with certain major known climatic events (e.g. past glaciations in Europe), a causal determination cannot *a priori* be assumed.

Both hypotheses have merely – even if limited – explanatory power to reconstruct the evolutionary scenario(s) under which cave adaptation may have occurred in each specific case.

Why live underground? From exaptation to adaptation

Subterranean life has played a significant role in shaping its inhabitants through evolutionary trends most often characterized by reduction, which has been studied since the earliest observations of cavernicolous animals (Racovitza 1907; Barr 1968; Culver 1982; Gibert and Deharveng 2002; Romero 2009; Mammola 2019, etc.). Troglomorphic insects, specifically, are known for exhibiting notable reductions in pigmentation, eye and wing sizes in adult individuals (Culver and Pipan 2018), but also specializations including elongated appendages, the development of specialized sensory organs, and an extended lifespan (Hoch 1994; Hoch 2002). Indeed, while most apparent traits for subterranean planthoppers involve such reduction or loss of certain morphological characteristics compared to their adult epygean relatives, other features with presumed increased adaptive value have also been suggested (Wessel et al. 2007). For example, Howarth (1981) described a specialized spine configuration on the tarsi of Hawaiian cavernicolous species of *Oliarus*, to enhance the insect's ability to walk on wet rocky surfaces. Another example is the Malagasy species *Tsingya clarkei* Hoch & Wessel, 2014, which exhibits a potential case of insular gigantism or autapomorphic giantism (Gould and MacFadden 2004) with the size of the species being more than twice larger than the other species of the family. However, in that specific case more than due to cavernicoly adaptation, the authors hypothesized this specialization as the possible result of a relaxation of predation and competition pressures together with random genetic drift (Keogh et al. 2005; Hoch et al. 2014).

Another interesting specialized pattern observed in several cave planthoppers is the heightened activity of the tegumentary gland system, responsible for wax production. These wax glands are also found in larger quantities, particularly in the tegmina and peripheral membrane of species such as *Valenciolenda fadaforesta*, *Solonaima baylissa*, *Ibleocixius dunae*, and *Typhlobrixia namorokensis* Synave, 1952. The hypertrophy of the glandular system (Hoch 2002) and increased complexity of chemosensory systems

(Balart-Garcia et al. 2022) could be correlated with the enhanced sensory function often observed in cave-dwelling organisms.

From a physiological perspective, cave planthoppers have undergone adaptations that render them indifferent to significant circadian and direct seasonal fluctuations, much like other true troglobitic species (Howarth and Moldovan 2018b). In turn, they have adapted to the absence of light, high and stable humidity levels, constant temperatures, and a scarcity of food resources restricted to the presence of roots in caves. As a result, these species have developed effective dispersal behaviors for locating food resources, relying more on walking than flying in total darkness. However, in open spaces, they sometimes exhibit a unique avoidance behavior resembling a parachute escape, where they jump followed by a gliding flight without wing beats, as observed in the recently discovered Spanish species *Valenciolenda fadaforesta*, and in the Australian cixiid species *Solonaima baylissa*, found in Queensland lava tubes (Hoch and Howarth 1989b). This behavior described as "parachuting", allows them to evade predators without straying too far from their rare and valuable food sources (Hoch et al. 2021).

However, while direct influences of seasonal fluctuations are excluded, there are slight and gradual indirect modifications of temperature and humidity that still regulate the seasonal distribution of insects within the MSS (Mesovoid Shallow Substratum) and floodable spaces. Moreover, the seasonal physiology of epigean plants through their roots might also influence seasonal patterns in the biology of planthoppers in an environment that still presents low seasonal fluctuations and is not completely stable (Lawton and Lawton 1971; Furukawa et al. 2011; Miller et al. 2020; Losso et al. 2023).

Alongside reporting morphological and physiological adaptations to underground life, it was assumed that subterranean environment was too "harsh" to be colonized without any preadaptation of its colonizers (Christiansen 1992; Holsinger 2000). On this same line, several authors (Oromí 2004; Giachino and Vailati 2005, 2006, 2010, 2016; Moseley 2009; Monguzzi 2011; reviewed in Mammola et al. 2016), have suggested that MSS should be regarded as the primary habitat for the subterranean fauna, a first step to the colonization to the MSP. Accordingly, MSS should be considered 'part of the hypogean ecosystem and represents its extension toward the surface' (Mammola et al. 2016). Romero (2009), however, questioned this notion of preadaptation ‹accepted without question' in biospeleogical publications, and showed that characters, supposed to be "pre-adaptations", in related fish taxa for instance, are not statistically significant to conclude that they were the main driver to cave colonization. From a theorical perspective, Gould and Vrba (1982) developed the concept of exaptation as an opportunistic selective adaptation, favoring traits that would become useful for a new function, for which they were not initially selected. Some planthopper troglomorphies have been considered as exaptations that likely facilitate subterranean colonization by organisms (Hoch 2002; d'Urso and Grasso 2009).

Contrasting evolutionary patterns in planthoppers: the Cixiidae case

With a few exceptions, only two main independent lineages, the Cixiidae and the Meenoplidae-Kinnaridae, have successfully colonized underground ecosystems. These

lineages are considered groups of epigean species whose larval instars are well known to feed on roots (Hoch 2002; Wessel et al. 2007; Bowser 2014; Bartlett et al. 2018). Both lineages exhibit exaptations in their larval instars for root feeding in the interstitial environment, enabling them to completely switch entirely to an endogeic life. However, the collected data reveal contrasting patterns: 50% of the described cave species belong to the Cixiidae, with 44 species out of more than 2600 species (1.6%), while the Meenoplidae-Kinnaridae comprise 21 species out of 285 species (7.3%) (Bourgoin 2023b). These patterns raise some interesting questions:

Why do other planthopper taxa with similar behavior and ecology, such as Tettigometridae, which are well-known root feeders and are often tended by ants underground (Bourgoin et al. 2023b), lack troglobiont representatives? Did Tettigometrids fail to undergo the necessary adaptations to thrive in subterranean environments? Could it be that the availability of suitable resources, physiological adaptations, and dispersal capabilities did not align within this particular lineage? Why are there so few cave-dwelling Delphacidae, or Derbidae or Achilidae although the nymphs of many species live close to the soil? Even more generally, why are there no cavernicolous Cicadomorpha at all? At least in the Cicadoidea (Cicadidae and Tettigarctidae) and Cercopidae one should expect some, as their nymphs also live underground, feeding on roots (Strümpel 2010, and references therein).

The presence of blind and unpigmented cixiid nymphs feeding on subterranean roots could indeed be considered as a potential exaptation, providing a foundation for the evolution of complete subterranean life. The cryptic, or even subterranean lifestyle of their nymphs is probably a specific trait of the family Cixiidae (Asche 1988). Could we consider Cixiidae as a subtroglophile lineage? Why then, however, are there only 44 species of Cixiidae which have successfully made the shift to cavernicoly? Which are the additional factors at play, beyond the initial exaptation, that determine or block the colonization and persistence of species in subterranean habitats? An example is the cixiid genus *Hyalesthes* Signoret, 1865 from the Canary Islands which is represented with several only epigean species throughout the archipelago (Hoch and Remane 1985). Adult *Hyalesthes* individuals are frequently observed in caves, however, apparently without establishing permanent subterranean populations (Hoch, unpublished). In contrast, other cixiid taxa, *Cixius* Latreille, 1804 and *Tachycixius* Wagner, 1939, while rare in surface habitats, have brought forth several separate lineages which have adapted to the subterranean biome (Hoch and Asche 1993).

How physiological adaptations specific to subterranean life, such as modifications in sensory systems, metabolism, or reproductive strategies of the different cixiid lineages, may also play a crucial role in successful colonization? Additionally, how the ability to disperse and establish populations in subterranean environments may have been influenced by dispersal capabilities, geographic barriers, or interactions with other organisms in the underground ecosystem?

While in theory, any cixiid species could potentially undergo an adaptive shift and make the transition to an entirely subterranean lifestyle, it is essential to critically analyze how exaptations take place: special morphological or behavioral traits might be necessary or not or but not sufficient in determining the success or failure of species in colonizing subterranean habitats.

Conclusions

According to the bioclimatic model proposed by Howarth (1980), terrestrial troglobites, can be expected "in any region which is old enough and in which there are extensive caves with an adequate moisture supply and a continuous equitable environment and food supply for colonization" (Howarth 1980: 403). Cave-dwelling planthoppers are found in many parts of the world (Fig. 1), and new species are continuously being discovered. Their occurrence is not limited to the current occurrence of related epigean taxa. They can thus shed light on past distribution of their lineages, leading to interesting questions of biogeography, regardless of climatic changes.

Planthoppers are a highly diverse taxon, occurring in a wide variety of habitats and climatic zones. This makes them ideal models for the study of troglobiont evolution. Comparative studies of nymphal morphology, biology and behavior of cixiids and meenoplidkinnarids, the latter being virtually unknown, may provide deeper insights in the ground pattern of Fulgoromorpha and eventually, a more complete picture of the factors leading to the evolution of troglobiont taxa. Specifically, the singularity of cavernicolous lineages within otherwise epigean clades (e.g, the genus *Notuchus* with 3 troglobiont species, within the Delphacidae, *Budginmaya eulae* within the Flatidae) and the phylogenetically isolated *Hypochthonella caeca* (being the only species of the Hypochtonellidae), deserves to be studied in depth, particularly from a phylogenetical perspective.

Apart from the evolutionary point of view, the existence of cavernicolous taxa raises attention to issues of conservation. Underground habitats are characterized by environmental stability, high humidity, and darkness (Poulson and White 1969; Culver 1982; Souza Silva et al. 2015; Sanchez-Fernandez et al. 2018). The inhabitants of these ecosystems are highly adapted to these conditions, and any disturbances can have detrimental effects on the associated fauna. Culver and Pipan (2010) demonstrated how abiotic changes in surface ecosystems can lead to the colonization of subterranean habitats. However, the indirect impacts of these changes on the underground world can be "fatal" to the existing cave inhabitants (Trajano 2000). The causes of such changes can be diverse, and many human activities have implications for the subterranean realm (Ferreira and Horta 2001; Faille et al. 2015b; Monro et al. 2018; Costa Cardoso et al. 2021). In the actual context of a biodiversity crisis, the question of the conservation of these ecosystems and their inhabitants is a priority. In line with this reflection, a cave conservation index of priority has been suggested (Souza Silva & al., 2015) and a roadmap to follow (Wynne et al. 2021). The cave-dwelling planthoppers are no exception, and already new conservation status have been published for some species (Santos et al. 2018; Borges et al. 2019; Hoch et al. 2021). Such actions will allow to better preserve the subterranean biome and collect data on their specialized, endemic and narrow range faunas, including planthoppers and other invertebrates.

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